

Stacking the odds: light pollution may shift the balance in an ancient predator–prey arms race

Running title: Lights alter predator–prey interactions

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Accepted version of article published in Journal of Applied Ecology

Please cite as follows:

Minnaar, C., Boyles, J.G., Minnaar, I. a., Sole, C.L. & McKechnie, A.E. (2015) Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. *Journal of Applied Ecology*, 52, 522–531.

SUMMARY

1. Artificial night-lighting threatens to disrupt strongly conserved light-dependent processes in animals and may have cascading effects on ecosystems as species interactions become altered.

Insectivorous bats and their prey have been involved in a nocturnal, coevolutionary arms race for millions of years. Lights may interfere with anti-bat defensive behaviours in moths, and disrupt a complex and globally ubiquitous interaction between bats and insects, ultimately leading to detrimental consequences for ecosystems on a global scale.

2. We combined experimental and mathematical approaches to determine effects of light pollution on a free-living bat–insect community. We compared prey selection by Cape serotine bats *Neoromicia capensis* in naturally unlit and artificially lit conditions using a manipulative field experiment, and developed a probabilistic model based on a suite of prey-selection factors to explain differences in observed diet.

3. Moth consumption by *N. capensis* was low under unlit conditions (mean percentage volume \pm SD: $5.91 \pm 6.25\%$), while moth consumption increased six-fold (mean percentage volume \pm SD: $35.42 \pm 17.90\%$) under lit conditions despite a decrease in relative moth abundance. Predictive prey-selection models which included high-efficacy estimates for eared-moth defensive behaviour found most support given diet data for bats in unlit conditions. Conversely, models which estimated eared-moth defensive behaviour as absent or low, found more support given diet data for bats in lit conditions. Our models therefore suggest the increase in moth consumption was a result of light-induced, decreased eared-moth defensive behaviour.

4. *Policy implications.* In the current context of unyielding growth in global light pollution, we predict that specialist moth-eating bats and eared-moths will face ever-increasing challenges to survival through increased resource competition and predation risk, respectively. Lights should be developed to be less attractive to moths, with the goal of reducing effects on moth behaviour. Unfortunately, market preference for broad-spectrum lighting and possible effects on other taxa make development of moth-friendly lighting improbable. Mitigation should therefore focus on the reduction of temporal, spatial, and luminance redundancy in outdoor lighting. Restriction of light inside nature reserves and urban greenbelts can serve as dark refugia for moth-eating bats and moths, and may become important for their persistence.

Keywords: arms race; Cape serotine bat; coevolution; eared moth; light pollution; *Neoromicia capensis*; predator–prey interactions; prey selection; Lepidoptera

INTRODUCTION

The nature of our planet’s orbit around the sun and rotation around its own axis are fundamental in contributing to the evolution of complex life on earth. Earth’s astronomical context, and the resulting fluctuations in ambient light, has led nearly all organisms to adapt to diel, monthly, and annual ambient light (solar, lunar, and celestial) cycles (Gaston *et al.* 2013). Extant ecosystems are therefore strongly governed by light and rely on historically consistent variations in ambient light for ecosystem function and stability (Kronfeld-Schor & Dayan 2003; Gaston *et al.* 2013). The recent introduction of artificial night-lighting by humans threatens to destabilise ecosystems by altering light-dependent biological processes for organisms as well as altering the availability of light and darkness as resources of energy, information, and refuge (Gaston *et al.* 2013).

Total night-time surface brightness on earth has nearly doubled from 1992 to 2012 (calculated from: Elvidge *et al.* 2014). This alarming trend shows little sign of abating as an additional 1,527,000 km² of land (an area more than three times the size of Madagascar) is predicted to be urbanised, worldwide, by 2030 (Seto *et al.* 2011). More alarmingly, at least 60% of this urban expansion is predicted to occur within 50 km of the boundaries of currently protected areas, as well as inside biodiversity hotspots (Güneralp & Seto 2013), making the spread of light pollution into previously unlit, and species-rich environments, inevitable. It is therefore pertinent to examine the effects of light pollution on vital ecosystem processes such as trophic interactions.

Bats and their insect prey are nocturnal, near-ubiquitous in their global occurrence, and have evolved complex predator–prey interactions across a timespan of 65 million years (Conner & Corcoran 2012). Several groups of insects, most notably moths, evolved ultrasound-sensitive ears to detect bat predators (Conner & Corcoran 2012). Moth ears are most sensitive to echolocation calls of common, sympatric bat species (typically 20–50 kHz), allowing them to detect these predators and avoid predation through evasive flight-manoeuvres, aposematic signals, or echolocation-jamming calls (Conner & Corcoran 2012). Syntonic bats produce echolocation calls that are readily detectable by moths and therefore tend to consume very few moths as part of their diet (Schoeman & Jacobs 2003, 2011). Allotonic bats have evolved echolocation frequencies that fall outside peak sensitivity of moth hearing range, or are of such low amplitude that moths are unable to detect pursuing bats with enough time to successfully evade capture (Goerlitz *et al.* 2010). Allotonic bats are able to circumvent eared-moth defences and often consume moths as their main prey (Schoeman & Jacobs 2003, 2011).

Nocturnally flying insects use celestial cues to navigate (Warrant & Dacke 2011), and this behaviour is disrupted by irrelevant cues introduced by artificial lights, causing attraction to light sources (van Langevelde *et al.* 2011). Apart from the attractant effect of lights, some eared moths show reduced defensive responses to simulated echolocation calls when exposed to light (Svensson & Rydell 1998; Svensson *et al.* 2003). Bat–moth interactions may thus be altered by light pollution as it could interfere with eared-moth defences, allowing syntonic bats, which often exploit congregations of insects around lights (Rydell 1991), to more successfully prey on eared-moths. Although individual syntonic bats generally consume few moths, the collective historical predation pressure on moths by syntonic bats has been strong enough to maintain morphological and behavioural adaptations against bat predation (Conner & Corcoran 2012). Therefore, introduced light may increase already significant levels of predation, possibly reducing moth populations in lit areas. If moths are a limiting resource for allotonic bats, light pollution may also pose an indirect threat to their survival.

To evaluate effects of light pollution on predator–prey interactions of bats and insects, we introduced an artificial light treatment in a naturally unlit area and measured differences in relative abundance of insect prey and relative prey consumption by bats between unlit and lit conditions. Although an *in situ* approach to test the effects of light pollution on community ecology is clearly warranted, such an approach limits the ability to directly measure predator–prey interactions and the various factors involved in prey selection. We therefore supplemented our field experiment with a mathematical approach and developed a predictive model framework based on prey-selection theory. The prey-selection model computed outcomes of multiple, hypothetical prey-selection scenarios which were compared to actual prey selection. This allowed for insight into possible mechanisms that determined prey selection in our study, and

allowed us to determine whether light pollution could potentially disrupt predator–prey interactions and perhaps permanently alter the balance in a global coevolutionary arms race.

MATERIALS AND METHODS

Study Site:

We conducted this study at Rietvlei Nature Reserve (RNR; 25°52'S; 28°15'E; ±1500 m.a.s.l.) in South Africa during late austral summer (February to April) of 2010 and 2011. There are no artificial light sources within the 40 km² area of RNR at night.

Experimental Design:

We altered naturally dark conditions found at RNR by introducing artificial lighting. This resulted in two experimental conditions: unlit (control) and lit (light pollution treatment). We used mercury-vapour lamps (HWL 160 W 220 V, Osram, Munich, Germany, see Fig. S1 for spectral composition) for our light pollution treatment, as the emission spectrum of these lamps is broadly inclusive of those of most current and emerging lighting technologies.

We placed one lamp on each of five lampposts with lights left on during lit conditions and switched off during unlit conditions (Fig. 1. a. i., 1b. vi). We alternated unlit and lit conditions in a six-day experimental cycle which was repeated 11 times (Fig. 1. d). We only collected data on day 1 and 4 of each cycle to allow bats to become accustomed to alternating conditions and avoid an overlap in insect remnants in bat digestive tracts between experimental conditions. Lit conditions were not induced within six days of full moon to avoid the decreased effect of lights on insect behaviour.

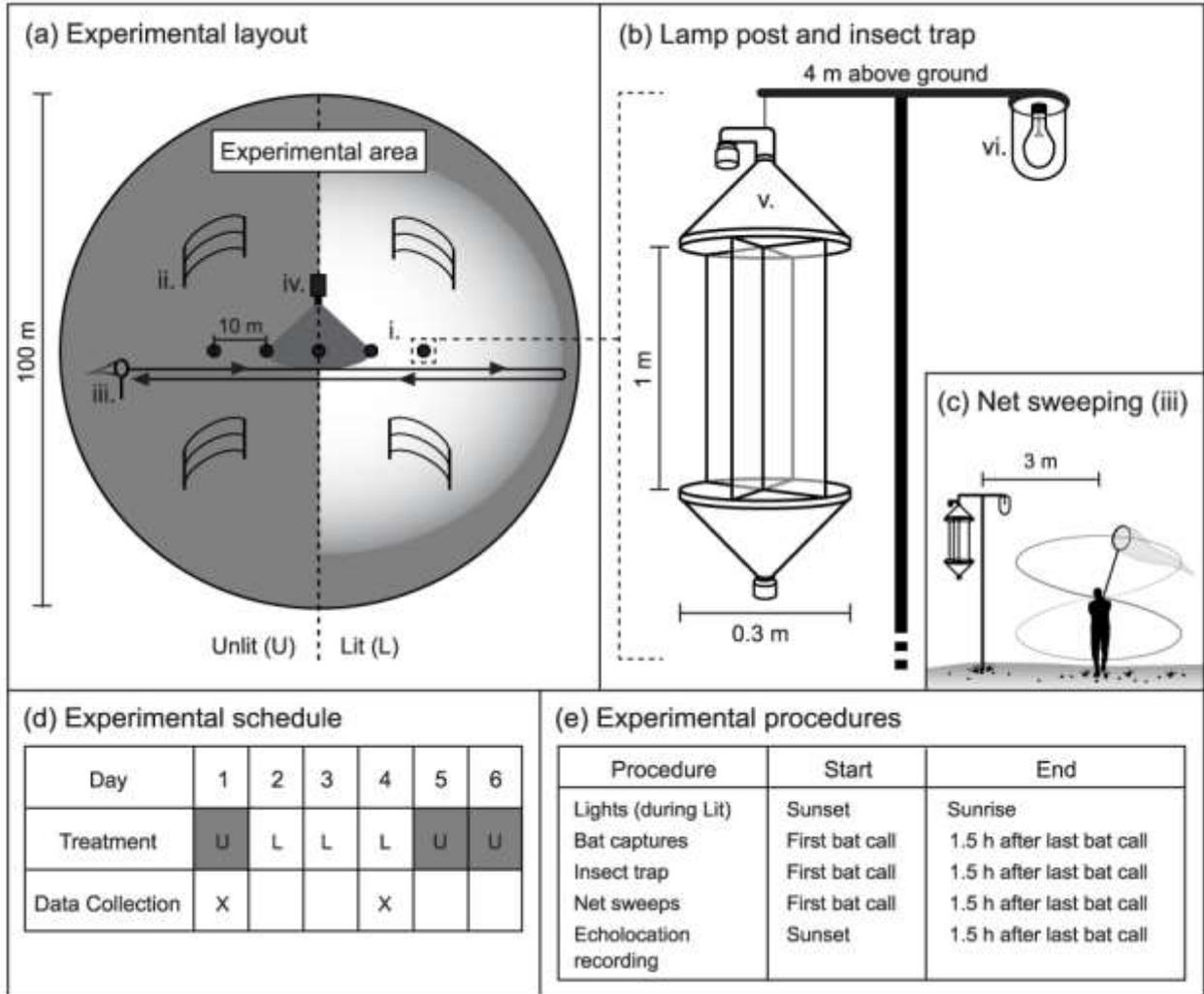


Figure 1. Graphical representation of the experimental design showing (a) the physical experimental layout and data collection techniques used, (b) equipment attached to each lamp post, (c) illustration of net sweeping procedure, (d) experimental schedule, and (e) experimental procedure details. The hand net (a. iii, c) had a 0.5 m diameter opening and was swept at a constant speed along a transect every 15 minutes. Omnidirectional traps (b. v) captured insects flying into clear Perspex® panes and funnelled them into collection jars above or below. We powered mercury vapour lamps (b. vi) with a quiet-operation generator (Honda Generator EU10i, Honda Motor Company Ltd., Berkshire, United Kingdom) placed outside the experimental area. The generator was also operational during unlit conditions to ensure similar acoustic conditions for both experimental conditions. We used an Anabat™ SD2 (Titley Electronics, Ballina, Australia) to record echolocation activity (a. iv).

We captured syntonic Cape serotine bats *Neoromicia capensis* A. Smith 1829 ($n = 11$ during unlit and $n = 12$ during lit) (peak echolocation call frequency: 39 kHz; call bandwidth: 14.4 kHz; call duration: 5.1 ms) (Monadjem *et al.* 2010) in mist nets during both experimental conditions (Fig. 1. a. ii). We held bats in cloth bags for 1–3 hours, wing punched them for future identification, and assigned a unique reference code to faecal samples to allow blind analysis. We sampled insect abundance using two non-attractant methods: 1) a hand net (Fig. 1. a. iii, 1. d), and 2) five omni-directional impaction traps (Kunz 1988) at lampposts (Fig. 1. b. v). We recorded and analysed bat echolocation activity to confirm foraging by *N. capensis* during experiments (Fig. 1. a. iv) (see Appendix S1. a in Supporting Information for details).

Data Processing and Analyses:

Diet Composition

We pooled faecal samples from individual bats (Whitaker, McCracken & Siemers 2009) and separated insect remains to order-level using a taxonomic reference text (Scholtz & Holm 1996) and comparison to insects caught during sampling. We estimated percentage volume composition of faecal contents to the nearest 5% for each insect order (Whitaker, McCracken & Siemers 2009). Dietary analyses based on faecal contents are influenced by biases related to digestibility of different prey items. However, the reliability of this methodology has been well established (Whitaker, McCracken & Siemers 2009), and results obtained are comparable to those obtained from molecular dietary analyses, which are theoretically robust to the effects of digestion (Goerlitz *et al.* 2010). Further, we do not expect digestibility of prey items to change between experimental conditions, and therefore, any bias should be the same between treatments.

Insect Abundance

We pooled all insects sampled for each sampling night to allow direct comparison with dietary composition of bats caught on that night. We sorted sampled insects to order-level and calculated relative abundance (%) for each. Finally, we classified moths as eared/non-eared based on family-level presence of ears (Scoble 1992) and verified the presence of tympanic organs under a microscope.

Statistical Procedures:

All proportional data were arcsine-transformed. To test for statistically significant differences between unlit and lit conditions, we used two-sample, independent *t*-tests (two-tailed). We conducted all statistical analyses in SPSS Statistics 17.0 (SPSS Inc., Chicago, IL).

Predictive Prey-Selection Model:

Model Conception

We built a theoretical model to predict diet of a bat based on five interacting factors: (1) relative prey abundance; (2) prey detectability and perception bias of the predator; (3) prey escape behaviour; (4) active selection of prey; and (5) physical handling constraints of prey. We predicted the representation of each insect order in each bat's diet using a set of models built on combinations of prey-selection factors and their selection probabilities, calculated from data collected during experiments and from literature. Below we provide a brief account of our conceptualisation, methods and hypotheses for each prey selection factor. Detailed methods for the calculation of selection probabilities for each prey selection factor are outlined in Appendix S1. b.

Probability of Prey Encounter (R)

A primary factor in prey selection is the probability that a predator will encounter specific prey during foraging (R) (Whitaker, McCracken & Siemers 2009). We hypothesised higher encounter rates of prey would increase the probability of those prey being consumed by a bat. Encounter probabilities for different prey orders were estimated from prey relative-abundance sampled during experiments (Appendix S1. b. i).

Probability of Prey Detection (D)

Sensory biases of predators affect the likelihood of different prey being detected (Safi & Siemers 2010). We used echolocation models (Safi & Siemers 2010; Stilz & Schnitzler 2012) to calculate the maximum detection distance of prey as a function of prey size, echolocation frequency, and atmospheric conditions. Maximum detection distance for a prey order on a given night was translated to a probability of detection by echolocation ($D_{(e)}$) (Appendix S1. b. ii). We hypothesised that increased detectability of prey through echolocation would result in an increased likelihood of consumption by bats.

During lit conditions, increased light may allow bats to use visual information as well as echolocation to capture prey. We calculated the visual detection probability of prey during lit conditions using estimated visual acuity of *N. capensis* and prey size data (Appendix S1. b. ii). We combined visual detection probabilities of prey with probabilities of detection using echolocation to determine the overall detection probability for prey ($D_{(ev)}$). If moths are more visually conspicuous than other prey, such as beetles, bats using vision in conjunction with echolocation under lit conditions may make moths more vulnerable to predation than other prey. We therefore also calculated the combined detection probability of prey orders, assuming moths

were three times more conspicuous than other prey ($D_{(ev-lep3)}$). This assumption provides a robust means of testing whether increased visual information caused moths, in particular, to be more vulnerable to predation. We assume vision was not used for prey capture during unlit conditions.

Probability of Capture Given Prey Evasive-Behaviour (E)

The reduction in bat predation through eared-moth defensive behaviours is estimated at 40% (Conner & Corcoran 2012). However, this estimate is based on experiments which were conducted under the influence of artificial lights and only accounted for secondary defensive behaviours (e.g. drastic defensive manoeuvres or echolocation-jamming) and not primary defensive behaviours (negative phonotactic flight relative to approaching bats). As a result of this uncertainty, we hypothesised four percentage efficacy-estimates (ee) for E : 20%, 40%, 60%, 80% (denoted as $E_{(20)}$, $E_{(40)}$, $E_{(60)}$, $E_{(80)}$) and incorporated these into our calculation of probability of capture given prey evasive-behaviour, E (Appendix S1. b. iii). The different levels of efficacy allowed us to test our hypothesis that eared-moth defences are reduced under lit conditions by comparing the performance of models containing different E variables between unlit and lit conditions. We also hypothesised that eared-moth defensive behaviours may be absent ($E_{(abs.)}$) (mathematically, models with no eared-moth defensive behaviours contain no selection probability for E).

Probability of Prey Being Actively Selected by the Predator (A)

Animals should select prey that maximise their net-energy gain (Emlen 1966; MacArthur & Pianka 1966). Since it is unlikely that bats have exact knowledge of prey energy-content, bats probably evolved a preference for sensory proxies of energy content such as taste or size (Schaefer, Spitzer & Bairlein 2008). Prey size is likely the simplest proxy bats could use for

prey energy-content. However, bats may also use other cues which would allow them to select more directly for prey energy-content. We thus considered both size- and energy-based selection in our models.

We calculated preference for prey based on size from body-length measurements for each insect order sampled during experiments on a particular night (Appendix S1. b. iv). We hypothesised size-preference would scale positively and linearly with prey size (Cunningham, Ruggerone & Quinn 2013). We calculated preference for prey from energy-content estimations from field-collected and literature data (Appendix S1. b. iv). We hypothesised that energy-preference would scale positively and linearly with prey energy-content.

A predator foraging in a high-quality patch should be more selective than a predator foraging in a low-quality patch (MacArthur & Pianka 1966). Therefore, the strength of preference, based on night-specific patch quality, was combined with size- or energy-preference to calculate the probability of active selection based on prey size ($A_{(s)}$) and energy ($A_{(e)}$) (Appendix S1. b. iv).

Probability of Prey Being Selected by the Predator Based on Handling Constraints (H)

We hypothesised that physical handling constraints of prey would limit consumption of prey. We related prey dimensions, and estimated hardness of prey to gape-size and bite-force estimates, as well as forearm length of individual bats to calculate the probability of successfully handling and chewing different prey available to each individual bat (Appendix S1. b. v).

Model Structure

Since selection probabilities were determined independently for each selection factor, we can combine them through simple multiplication to determine overall probability of different prey orders being consumed by bats. The complete model takes the following form:

$$C_{(x,ia)} = R_{ia} \times D_{ia} \times E_{ia} \times A_{ia} \times H_{ia} \quad (\text{eqn 1})$$

$C_{x,ia}$ is the probability of prey order i being consumed by bat a as predicted by model x .

Following this, predicted percentage-volume consumption of prey order i by bat a was calculated as follows:

$$V_{x,ia} = \left(\frac{C_{x,ia}}{[C_{x,ia} + C_{x,ja} + \dots + C_{x,qa}] } \right) \times 100 \quad (\text{eqn 2})$$

where the probability of consumption of prey order i by bat a , predicted by model x ($C_{x,ia}$), is divided by the sum of probabilities of consumption of all other prey orders by bat a predicted by model x . This is multiplied by 100 to obtain a predicted percentage consumption value ($V_{x,ia}$) for prey order i .

Models and Implementation

Each selection probability represents one or more hypotheses for each factor of prey selection. We created an ecologically realistic model-set from the global model (equation 1) using various combinations of factors. In accordance with ecological realism, all models contained encounter rate, detectability, and handling as factors. We included variations of prey defensive behaviour efficacy ($E_{(abs.)}$, $E_{(20)}$, $E_{(40)}$, $E_{(60)}$, $E_{(80)}$), active selection ($A_{(e)}$, $A_{(s)}$) and probability of detection ($D_{(e)}$, $D_{(ev)}$, $D_{(ev-lep3)}$) in different models. This resulted in a total of 15 models for unlit conditions and 45 models for lit conditions (Table S2). By calculating models for bat diets in lit and unlit

conditions separately, our model set allowed us to test multiple hypotheses regarding differences in diet between experimental conditions.

Each prey-selection model predicted the probability of selection of a specific insect order for an individual bat (Fig. 2. a), and thus predicted volume consumption of each order for each bat (equation 10) (Fig. 2. a). To assess the fit of models, we calculated sum of squared prediction errors (SSE) as follows:

$$SSE_{x,a} = \sum_{i=insect\ order\ 1}^{insect\ order\ 9} (V_{ia} - V_{x,ia})^2 \quad (\text{eqn 3})$$

where the squared difference between actual volume consumed of an insect order by a particular bat (V_{ia}), and consumed volume predicted for that insect order by model x ($V_{x,ia}$), is summed for all orders available to the bat in question. An SSE value was calculated for each bat (Fig. 2. b). SSE values were then averaged across all bats for each model to obtain the mean square error (MSE) for each model (Fig. 2. c). The entire analysis procedure described above was conducted for lit and unlit conditions separately.

We used the MSE of each model to calculate the second-order variant of Akaike's information criterion (AIC_c) for small sample sizes (Akaike 1973; Sugiura 1978) to assess model performance. We further assessed relative performance of models using AIC_c differences ($\Delta AIC_c = AIC_{cx} - AIC_{c\ min}$) and Akaike weights (w_i) for each model for unlit and lit conditions (Burnham & Anderson 2002). To interpret the relative importance of each factor in the model, we used the sum of w_i for models which contained or excluded the factor of interest (Burnham & Anderson 2002).

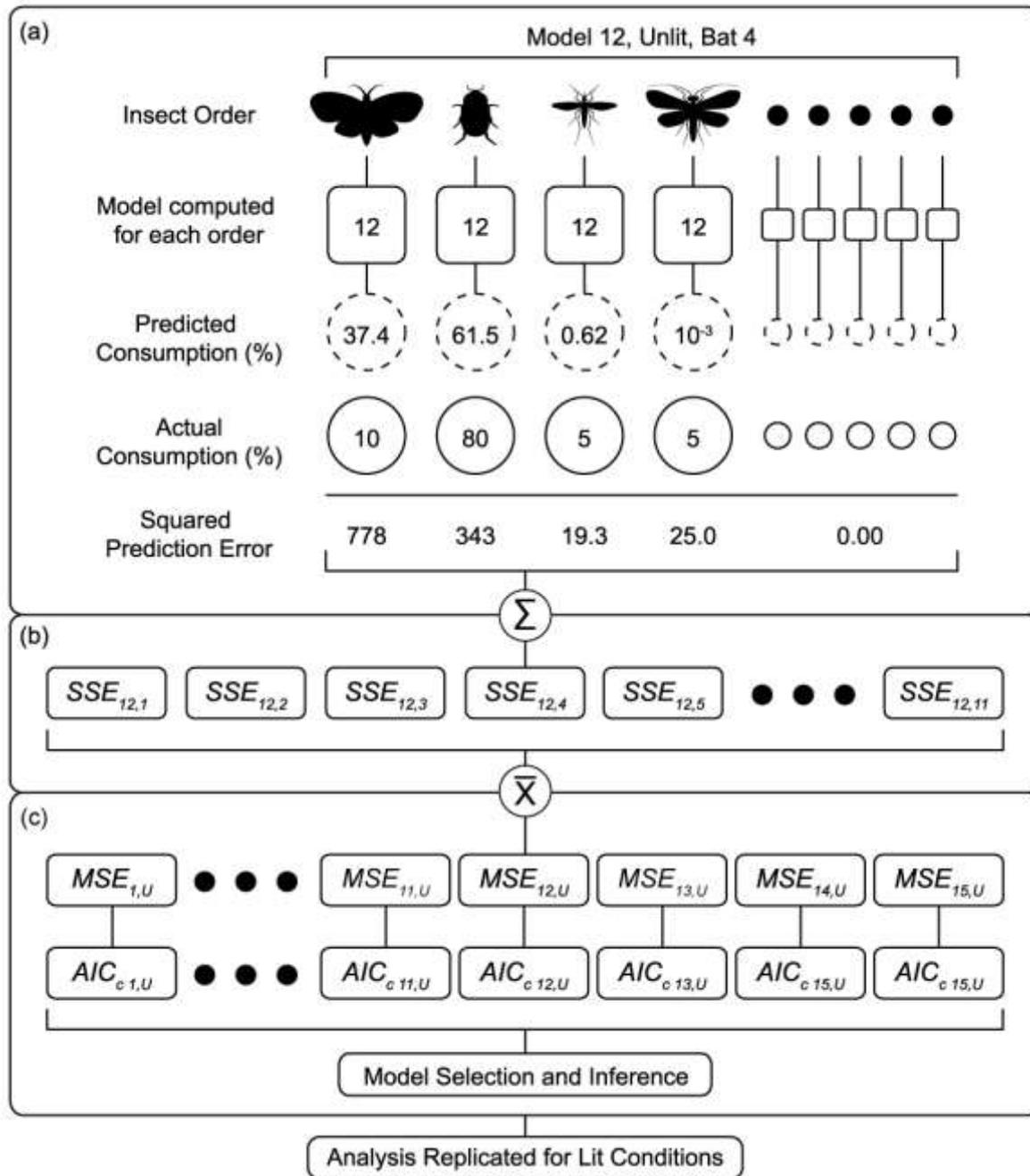


Figure 2. Schematic diagram of prey-selection model implementation. Panel a: an example of model 12 being computed for each insect order available to bat 4 on the night its diet was sampled; insect orders depicted by drawings are, from left to right: Lepidoptera, Coleoptera, Diptera, Trichoptera and others indicated by black dots. Panel b: Sum of squared errors (*SSE*) for each bat for a given model is obtained. Panel c: *SSE* values are averaged for a given model to estimate its overall prediction error and the resultant mean sum of squared prediction errors (*MSE*) are then analysed using the second order variant of Akaike's information criterion (*AIC_c*).

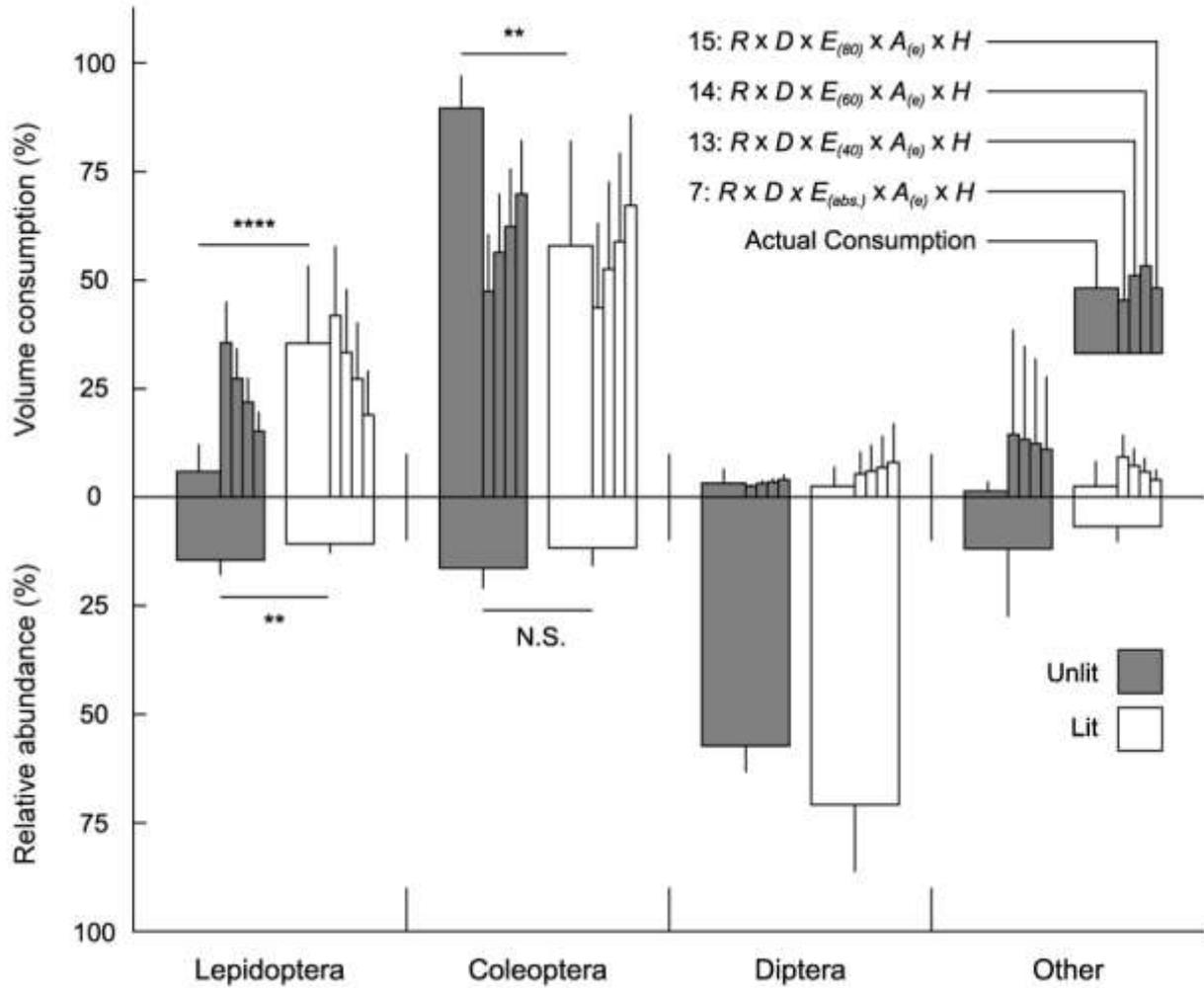


Figure 3. Histogram summary of relative abundance, as well as actual, and model-predicted, consumption of different prey orders by the syntonic bat, *Neoromicia capensis*, during naturally unlit (n = 11; grey bars) and artificially lit conditions (n = 12; white bars). Top thick bars indicate actual consumption of different prey orders during unlit and lit conditions. Model-prediction bars are placed in ascending order of prey evasive behaviour efficacy (E), next to actual consumption (wide bars) for comparison. Bottom bars indicate actual relative abundance of different prey orders for unlit and lit conditions. Bars indicate mean percentage with standard deviation indicated by error bars. Independent, two sample *t*-tests (two-tailed) comparison results are indicated by cross bars (N.S. no significant difference, ** $P < 0.01$, **** $P < 0.0001$).

RESULTS

Field Experiment

Bat activity (activity index: Miller 2001), was detected during both unlit and lit conditions (mean activity index $\% \pm$ SE: unlit = 19.60 ± 4.01 ; lit = 44.59 ± 9.78), but was significantly higher during lit conditions ($t = 2.812$, d.f. = 19, $P = 0.011$). *Neoromicia capensis* consumed mostly beetles (Coleoptera) under unlit conditions (Fig. 3). However, under lit conditions, bats consumed six times more moths than during unlit conditions ($t = 4.784$, d.f. = 21, $P < 0.0001$). Conversely, beetle consumption decreased significantly from unlit to lit conditions ($t = 4.196$, d.f. = 21, $P = 0.004$).

Moth relative abundance was significantly lower during lit conditions ($t = 2.945$, d.f. = 21, $P = 0.008$), whereas beetle relative abundance was not significantly different ($t = 1.643$, d.f. = 21, $P = 0.115$) (Fig. 3). Diptera were the most abundant prey but were not consumed in large numbers. Trichoptera were also present, but relatively scarce and consumed in small quantities only. Orthoptera, Hemiptera, Neuroptera, Hymenoptera, and Mantodea were present in small numbers and were not detected in bat diets. Eared moths comprised 92.9% ($n = 637$) of all moths sampled. Eared-moth abundance as a proportion of overall moth abundance was not significantly different between unlit (mean $\% \pm$ SD: 89.67 ± 4.71) and lit (mean $\% \pm$ SD: 92.94 ± 1.09) conditions ($t = 2.077$, d.f. = 21, $P = 0.0503$).

Predictive Prey-Selection Model

Model Predictions and Selection with AIC_c

Overall, all models predicted prey selection well, with the worst models achieving mean absolute prediction errors of ~17% and the best models < 5%. During unlit conditions, a model predicting

eared-moth evasive-behaviour efficacy at 80% and including active selection based on energy content by bats was the best model and received nearly complete support ($w_i = 0.84$) given our model-set (Table 1). Volume consumption predictions from this model closely matched actual consumption (mean absolute prediction error = $4.94 \pm 3.48\%$), although it over- and underestimated Lepidoptera and Coleoptera consumption, respectively (Fig. 3).

Table 1

Summary of five best predictive prey-selection models for *Neoromicia capensis* diet, during unlit and lit conditions. Model structures* are shown with the number of parameters (K), mean absolute prediction error (MAPE), AIC_c values, $\Delta AIC_{ci} = AIC_{ci} - AIC_c$ min, Akaike weights (w_i). Models are ranked by AIC_c values

Treatment and Model Number	Model Structure
Unlit:	
15	$R \times D_{(e)} \times E_{(80)} \times A_{(e)} \times H$
14	$R \times D_{(e)} \times E_{(60)} \times A_{(e)} \times H$
1	$R \times D_{(e)} \times E_{(abs.)} \times H$
7	$R \times D_{(e)} \times E_{(abs.)} \times A_{(e)} \times H$
13	$R \times D_{(e)} \times E_{(40)} \times A_{(e)} \times H$
Lit:	
7	$R \times D_{(e)} \times E_{(abs.)} \times A_{(e)} \times H$
14	$R \times D_{(e)} \times E_{(60)} \times A_{(e)} \times H$
13	$R \times D_{(e)} \times E_{(40)} \times A_{(e)} \times H$
12	$R \times D_{(e)} \times E_{(20)} \times A_{(e)} \times H$
15	$R \times D_{(e)} \times E_{(80)} \times A_{(e)} \times H$

* R = probability of prey encounter; D = probability of detection (subscript brackets (e) indicates detectability of prey using echolocation); E = probability of capture given prey evasive-behaviour (subscript brackets indicate level of prey evasion efficacy); A = probability of prey being actively selected by the predator (subscript brackets indicate active selection based on energy (e) and size (s) of prey); H = probability of prey being selected by the predator based on handling constraints

For lit conditions, the best model predicted no eared-moth defensive behaviour (Table 1).

Models that included active selection based on energy content, handling limitations, and various

levels of evasive behaviour were also moderately successful at predicting diet composition, although ΔAIC_c were > 3 in all cases. Models which included visual detection, including those which assumed moths were three times more visually conspicuous than other prey, were not well supported ($w_i < 0.03$)

Table 2

The sum of Akaike weights (w_i) for predictive prey-selection models, grouped by the presence or absence of prey-selection factors*, are shown for unlit and lit conditions. The summed Akaike weights (w_i) show the relative importance of each factor in accurately predicting diet for *Neoromicia capensis* under unlit and lit conditions

Models grouped by prey selection factor	Sum of Akaike weights (w_i)	
	Unlit	Lit
$E_{(abs.)}$	0.060	0.638
$E_{(20)}$	0.008	0.071
$E_{(40)}$	0.016	0.116
$E_{(60)}$	0.068	0.126
$E_{(80)}$	0.849	0.049
$A_{(s)}$	0.002	0.007
$A_{(e)}$	0.937	0.954
$D_{(e)}$	1.000	0.952
$D_{(ev)}$	NA	0.046
$D_{(ev-lep3)}$	NA	0.001

* E = probability of capture given prey evasive-behaviour (subscript brackets indicate level of prey evasion efficacy); A = probability of prey being actively selected by the predator (subscript brackets indicate active selection based on energy (e) and size (s) of prey

Overall, models which included highly efficient evasive behaviour by moths ($E_{(80)}$) were best at predicting diet for bats during unlit conditions (Table 2). Other levels of evasive behaviour by moths ($E_{(abs., 20,40,60)}$) were not well supported by diet data for bats during unlit conditions. Conversely, the evidence in support of models without eared-moth defensive

behaviour ($E_{(abs.)}$) were important in predicting diets of bats under lit conditions. The other four estimates of evasive behaviour received limited support for lit bat diet. Active selection based on energy ($A_{(e)}$) was important during both unlit and lit conditions, whereas selection based on size ($A_{(s)}$) received little support. Detection based on echolocation alone ($D_{(e)}$), received overwhelming support for lit conditions while the combination of echolocation and vision was not well supported ($D_{(ev)}$ and $D_{(ev-lep3)}$).

DISCUSSION

Neoromicia capensis consumed relatively few moths in natural darkness, likely because these bats are syntonic echolocators and thus audible to eared moths. Under artificially lit conditions, moth consumption increased drastically, although it is unclear from our experiment alone what drove this increase. Dietary composition clearly did not follow relative abundance of prey in either treatment, which confirms the need to assess other prey-selection factors to understand bat diets in our study.

Our model allows us, for the first time, to address the relative importance of several factors affecting prey selection in insectivorous bats. Notably, eared-moth defensive behaviour in unlit conditions and the absence of it in artificially lit conditions were important factors in predicting diet composition in *N. capensis*. Specifically, models estimating eared-moth defensive behaviour as 80% effective described data collected during unlit conditions well. Under lit conditions, the best model included no eared-moth defensive behaviour. The second ($\Delta AIC_c = 3.17$) and third ($\Delta AIC_c = 3.34$) most likely models estimated efficacy of defensive behaviour at 60% and 40%, respectively. These three models, which have a collective AIC weight of 0.801, all estimate the efficiency of eared-moth defensive behaviours as being lower than the best

model for unlit conditions. From this, we infer that during lit conditions, eared-moth defensive behaviour was lower than during unlit conditions, and possibly absent. The hypothesis that vulnerability of moths around lights is a result of increased visual information, and in particular increased visual conspicuousness of moths relative to other prey, is not supported by our data.

Active selection based on energy content was present in nearly all of the top models. This is unexpected as *N. capensis* are considered to be unable to distinguish among prey accurately, which is a logical prerequisite to energy-based selection (Barclay & Brigham 1994).

Alternatively, *N. capensis* may still be selecting prey based on size, but their preference scales exponentially with increasing prey size, more closely approximating selection for energy than size, as mass, and therefore energy content scales exponentially with increasing body size in insects (Sabo, Bastow & Power 2002). Our modelling framework therefore provides strong inferential evidence that active selection capabilities in low-duty-cycle echolocating bats are more developed than previously thought.

Ecological and Evolutionary Implications

The increase in moth consumption by syntonic bats around artificial lights may have substantial impacts on bat–moth coevolutionary arms races globally. Increasing urbanisation (Güneralp & Seto 2013) and subsequent introduction of artificial lights into previously unlit environments may allow syntonic bats access to an historically unavailable resource in eared moths. This may result in markedly increased and unprecedented pressures on eared-moth populations, possibly leading to conservation problems for these species. Moth abundance has declined sharply in Europe over the last few decades, and this may be due in part to increased light pollution (Fox 2013).

Although light pollution may benefit syntonic species, allotonic bat species may face increased resource competition because of their reliance on eared moths as a primary food resource (Schoeman & Jacobs 2003, 2011). Further, avoidance of lit environments has been found in several allotonic bat species (Rydell 1992; Stone, Jones & Harris 2009, 2012; Lewanzik & Voigt 2014). Light avoidance in bats is likely adaptive to avoid avian predation (Speakman 1991). Allotonic bats tend to be small, slow-flying, and have echolocation calls adapted for cluttered habitats (Schnitzler, Moss & Denzinger 2003), possibly increasing their actual and perceived risk of predation in artificially lit environments. Light pollution may therefore pose a formidable threat to allotonic bat survival by: 1) allowing syntonic bats access to a resource primarily limited to allotonic species in the past; 2) attracting prey away from cluttered foraging habitats of allotonic bats; and 3) possibly increasing perceived predation risk for allotonic species, and thereby excluding them from foraging in lit areas. More analyses of the effect of light pollution on sympatric, syntonic, and allotonic species are clearly needed to explore these predictions.

We provide the first experimental evidence, supported by prey-selection modelling, that even at a small scale, artificial light can have a significant, disruptive effect on trophic interactions between predators and prey, and may permanently alter a 65 million year old coevolutionary arms race involving more than 750 bat and 50,000 moth species (Wilson & Reeder 2005; Kristensen, Scoble & Karsholt 2007). Mitigation of the harmful effects of light pollution should be prioritised as a conservation measure for both eared moths and allotonic bats.

Policy and Management Recommendations

Different lighting technologies have different spectral compositions, which may be more or less attractive to moths. We could not confirm from our study whether a reduction in defensive behaviour efficacy is coupled with moth attraction to light. However, attraction to, and subsequent flight around lights, is a logical prerequisite for light to have an effect on moth defensive behaviour. Moreover, disorientation caused by light, may itself contribute to decreased defensive behaviour efficacy. Lighting technologies which are less attractive to moths are therefore less likely to reduce moth defensive behaviours. It is commonly thought that ultra-violet (UV) wavelengths are the cause of attraction to light in moths, but several recent studies have contradicted this notion (Pawson & Bader 2014; van Grunsven *et al.* 2014). Moths are strongly attracted to LED lights (no UV emissions) of various colour temperatures (Pawson & Bader 2014) as well as high-pressure sodium lights (negligible UV) (Perkin, Hölker & Tockner 2014). These findings clearly indicate moth attraction to light is not simply caused by UV wavelengths. Current understanding of moth attraction to light is poor (van Grunsven *et al.* 2014). With better understanding, lighting technologies which are less attractive to moths could potentially be developed in future, but these may still have detrimental effects on other taxa.

Consumers' lighting preferences are more likely to drive development of lighting technology than are conservation concerns for moths and bats. Unfortunately, human visual characteristics overlap with a wide number of taxa (Davies *et al.* 2013), and demand for lighting is driven by human preference for 'natural-looking' light (broad-spectrum), so it may ultimately be impossible to develop lighting technologies which are both ecologically neutral for all taxa and acceptable for consumers. For example, LED lights with broad spectra are increasingly being favoured for their 'white light' and low power consumption, but may increase the

disruptive power of light pollution on a variety of taxa (Davies *et al.* 2013; Pawson & Bader 2014). It seems clear that the development of lighting technologies with ecologically neutral spectra holds little promise, and should not be considered a priority conservation measure.

We recommend mitigation efforts focus on reducing temporal, spatial, and luminance redundancy of outdoor lighting. The integration of motion-sensing technology with street lighting would substantially reduce redundant lighting (Kyba, Hänel & Hölker 2014) and its impact on animals. Simple motion-activated switches could likewise be employed for building security lights and lighting along walkways. Despite the simplicity of this concept and technology required to implement it, roads, walkways and buildings around the world often remain fully lit during times when not used, and hence when lights are not needed.

Increasing lighting efficiency will reduce the energetic cost of lighting, but this may also allow for increased illumination at a lower costs. Legislation limiting light intensity needs to be established to avoid redundancy in brightness that is easily achievable with modern lighting technology (Kyba, Hänel & Hölker 2014). Careful planning and light-beam manipulation can reduce spatial redundancy in lighting and sky-glow. Dark refugia within the urban–rural matrix are likely important for the persistence of light-sensitive bat and moth species. Green belts and nature reserves should be kept free from lights to act as dark reserves at night. Careful planning and responsible use of lighting can simultaneously promote road, building and personal safety while minimizing energy costs and direct ecological impacts.

ACKNOWLEDGEMENTS

We thank Bat Conservation International and the South African National Research Foundation (grant number 74604) for financial support; Rietvlei Nature Reserve and Riaan Marais; Drs. Dale Sparks and Eric Britzke for bat detector loans. We also thank Dr Kamran Safi and two anonymous reviewers who provided constructive comments on an earlier version of the manuscript. All experiments reported herein were approved by the Animal Use and Care Committee of the University of Pretoria (protocol EC005-10).

DATA ACCESSIBILITY

- Diet and morphological data for individual bats: DRYAD entry doi:10.5061/dryad.48kc1 (Minnaar *et al.* 2015)

REFERENCES

- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. Akademiai Kiado, Budapest.
- Barclay, R.M.R. & Brigham, R.M. (1994) Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. *Animal Behaviour*, **48**, 1013–1021.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- Conner, W.E. & Corcoran, A.J. (2012) Sound strategies: the 65 million-year-old battle between bats and insects. *Annual Review of Entomology*, **57**, 21–39.
- Cunningham, C.J., Ruggerone, G.T. & Quinn, T.P. (2013) Size selectivity of predation by brown bears depends on the density of their sockeye salmon prey. *The American Naturalist*, **181**, 663–673.

- Davies, T.W., Bennie, J., Inger, R., de Ibarra, N.H. & Gaston, K.J. (2013) Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? *Global Change Biology*, **19**, 1417–23.
- Elvidge, C., Hsu, F.C., Baugh, K.E. & Ghosh, T. (2014) National trends in satellite observed lighting: 1992–2012. *Global Urban Monitoring and Assessment Through Earth Observation* (ed Q. Weng), pp. 97–120. CRC Press, Boca Raton.
- Emlen, J.M. (1966) The role of time and energy in food preference. *The American Naturalist*, **100**, 611–617.
- Fox, R. (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity*, **6**, 5–19.
- Gaston, K.J., Bennie, J., Davies, T.W. & Hopkins, J. (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological Reviews of the Cambridge Philosophical Society*, **88**, 912–27.
- Goerlitz, H.R., ter Hofstede, H.M., Zeale, M.R.K., Jones, G. & Holderied, M.W. (2010) An aerial-hawking bat uses stealth echolocation to counter moth hearing. *Current Biology*, **20**, 1568–1572.
- Van Grunsven, R.H.A., Donners, M., Boekee, K., Tichelaar, I., van Geffen, K.G., Groenendijk, D., Berendse, F. & Veenendaal, E.M. (2014) Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. *Journal of Insect Conservation*, **18**, 225–231.
- Güneralp, B. & Seto, K.C. (2013) Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environmental Research Letters*, **8**, 014025 (10pp).
- Kristensen, N.P., Scoble, M.J. & Karsholt, O. (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa*, **1668**, 699–747.
- Kronfeld-Schor, N. & Dayan, T. (2003) Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 153–181.
- Kunz, T.H. (1988) Methods for assessing prey availability for insectivorous bats. *Ecological and Behavioral Methods for the Study of Bats* (ed T.H. Kunz), pp. 191–210. Smithsonian Institution Press Washington, Washington D.C.
- Kyba, C.C.M., Hänel, A. & Hölker, F. (2014) Redefining efficiency for outdoor lighting. *Energy and Environmental Science*, **7**, 1806–1809.
- Van Langevelde, F., Ettema, J.A., Donners, M., WallisDeVries, M.F. & Groenendijk, D. (2011) Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, **144**, 2274–2281.
- Lewanzik, D. & Voigt, C.C. (2014) Artificial light puts ecosystem services of frugivorous bats at risk. *Journal of Applied Ecology*, **51**, 388–394.

- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist*, **100**, 603–609.
- Miller, B.W. (2001) A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, **3**, 93–105.
- Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L. & McKechnie, A.E. (2015) Data from: Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race, DRYAD, doi:10.5061/dryad.48kc1, <http://doi.org/10.5061/dryad.NNNNN>
- Monadjem, A., Taylor, P.J., Cotterill, F.P.D. & Schoeman, M.C. (2010) Species Accounts: Vespertilionidae. *Bats of Southern and Central Africa: A Biogeographic and Taxonomic Synthesis* (eds A. Monadjem, P.J. Taylor, F.P.D. Cotterill & M.C. Schoeman), pp. 464–467. Wits University Press, Johannesburg.
- Pawson, S.M. & Bader, M.K.-F. (2014) LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications*, **24**, 1561–1568.
- Perkin, E.K., Hölker, F. & Tockner, K. (2014) The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshwater Biology*, **59**, 368–377.
- Rydell, J. (1991) Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssonii*. *Ecography*, **14**, 203–207.
- Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, **6**, 744–750.
- Sabo, J.L., Bastow, J.L. & Power, M.E. (2002) Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, **21**, 336–343.
- Safi, K. & Siemers, B. (2010) Implications of sensory ecology for species coexistence: biased perception links predator diversity to prey size distribution. *Evolutionary Ecology*, **24**, 703–713.
- Schaefer, H.M., Spitzer, K. & Bairlein, F. (2008) Long-term effects of previous experience determine nutrient discrimination abilities in birds. *Frontiers in Zoology*, **5**, doi:10.1186/1742-9994-5-4.
- Schnitzler, H.U., Moss, C.F. & Denzinger, A. (2003) From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology & Evolution*, **18**, 386–394.
- Schoeman, C.M. & Jacobs, D.S. (2003) Support for the allotonic frequency hypothesis in an insectivorous bat community. *Oecologia*, **134**, 154–162.
- Schoeman, M.C. & Jacobs, D.S. (2011) The relative influence of competition and prey defences on the trophic structure of animalivorous bat ensembles. *Oecologia*, **166**, 493–506.
- Scholtz, C.H. & Holm, E. (1996) *Insects of Southern Africa*, 2nd ed (eds CH Scholtz and E Holm). Protea Book House, Pretoria.

- Scoble, M.J. (1992) *The Lepidoptera. Form, Function and Diversity*. Oxford University Press, Oxford.
- Seto, K.C., Fragkias, M., Güneralp, B. & Reilly, M.K. (2011) A meta-analysis of global urban land expansion. (ed JA Añel). *PloS one*, **6**, e23777.
- Speakman, J.R. (1991) Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology*, **5**, 518–524.
- Stilz, W.-P. & Schnitzler, H.-U. (2012) Estimation of the acoustic range of bat echolocation for extended targets. *The Journal of the Acoustical Society of America*, **132**, 1765–75.
- Stone, E.L., Jones, G. & Harris, S. (2009) Street lighting disturbs commuting bats. *Current Biology*, **19**, 1123–1127.
- Stone, E.L., Jones, G. & Harris, S. (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, **18**, 2458–2465.
- Sugiura, N. (1978) Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics- Theory and Methods*, **A7**, 13–26.
- Svensson, A.M., Eklöf, J., Skals, N. & Rydell, J. (2003) Light dependent shift in the anti-predator response of a pyralid moth. *Oikos*, **101**, 239–246.
- Svensson, A.M. & Rydell, J. (1998) Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera spp.*; Geometridae). *Animal Behaviour*, **55**, 223–226.
- Warrant, E. & Dacke, M. (2011) Vision and visual navigation in nocturnal insects. *Annual Review of Entomology*, **56**, 239–254.
- Whitaker, J.O., McCracken, G.F. & Siemers, B.M. (2009) Food Habits Analysis of Insectivorous Bats. *Ecological and Behavioral Methods for the Study of Bats*, 2nd ed (eds T.H. Kunz & S. Parsons), pp. 567–592. The Johns Hopkins University Press, Baltimore.
- Wilson, D.E. & Reeder, D.A.M. (2005) *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed. Johns Hopkins University Press, Baltimore.

SUPPORTING INFORMATION

Figure S1. Spectral composition of common outdoor lighting technologies compared to mercury vapour light

Figure S2. Comparison of model estimated detection capabilities of *N. capensis* using vision and echolocation

Appendix S1. Supplementary Methods

Table S1. Body length, estimated energy content, estimated maximum detection distance, and sampling rate shown for all insects captured during unlit and lit conditions, respectively

Table S2. Selection probability factors included in all models tested shown with number of parameters for each

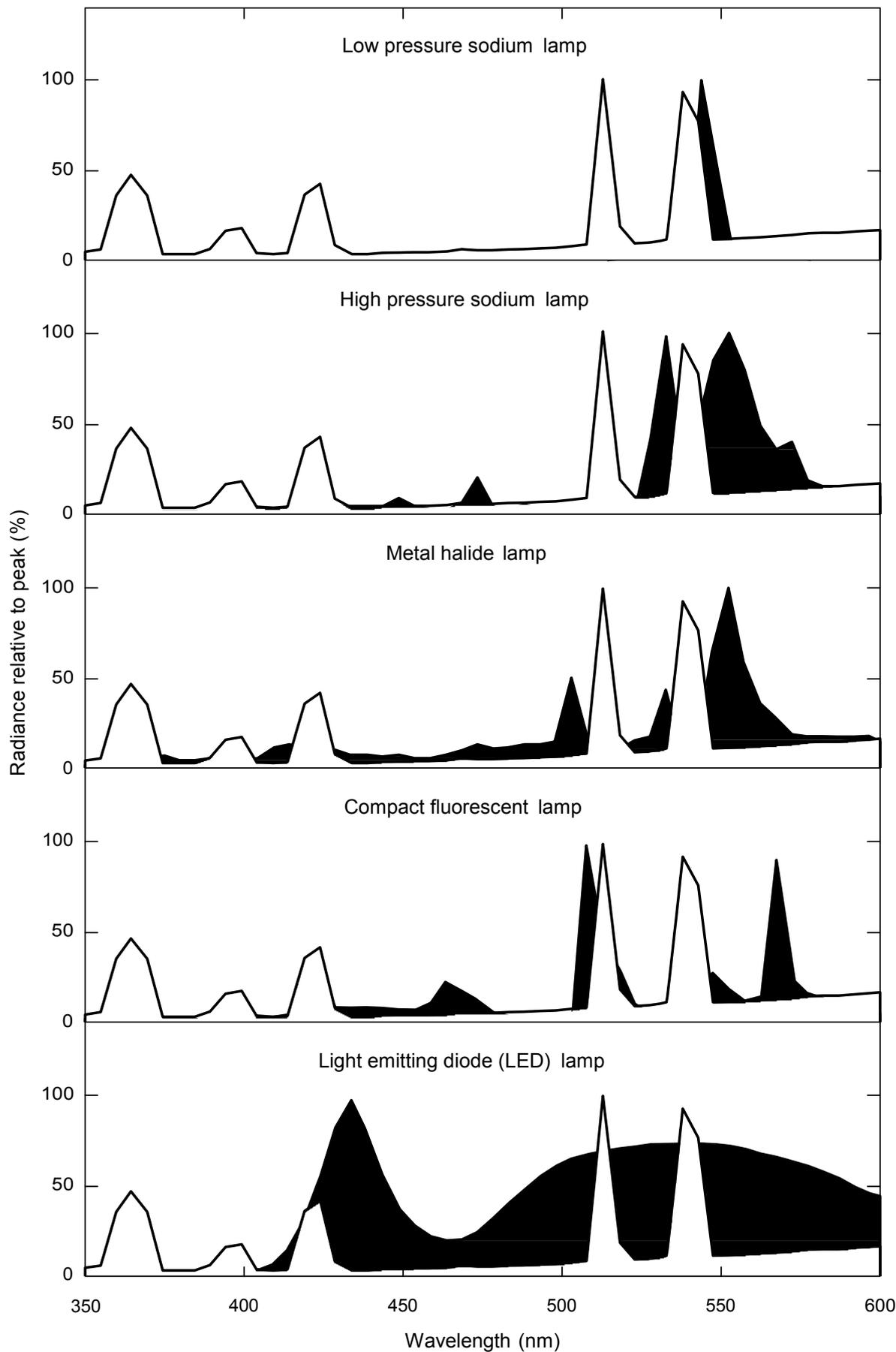


Figure S1. Emission spectra of various common outdoor lighting technologies (black) compared to that of a mercury vapor lamp (translucent white). Emission spectra were obtained from Elvidge et al., (2010).

Elvidge, C.D., Keith, D.M., Tuttle, B.T. & Baugh, K.E. (2010) Spectral identification of lighting type and character. *Sensors*, **10**, 3961–3988.

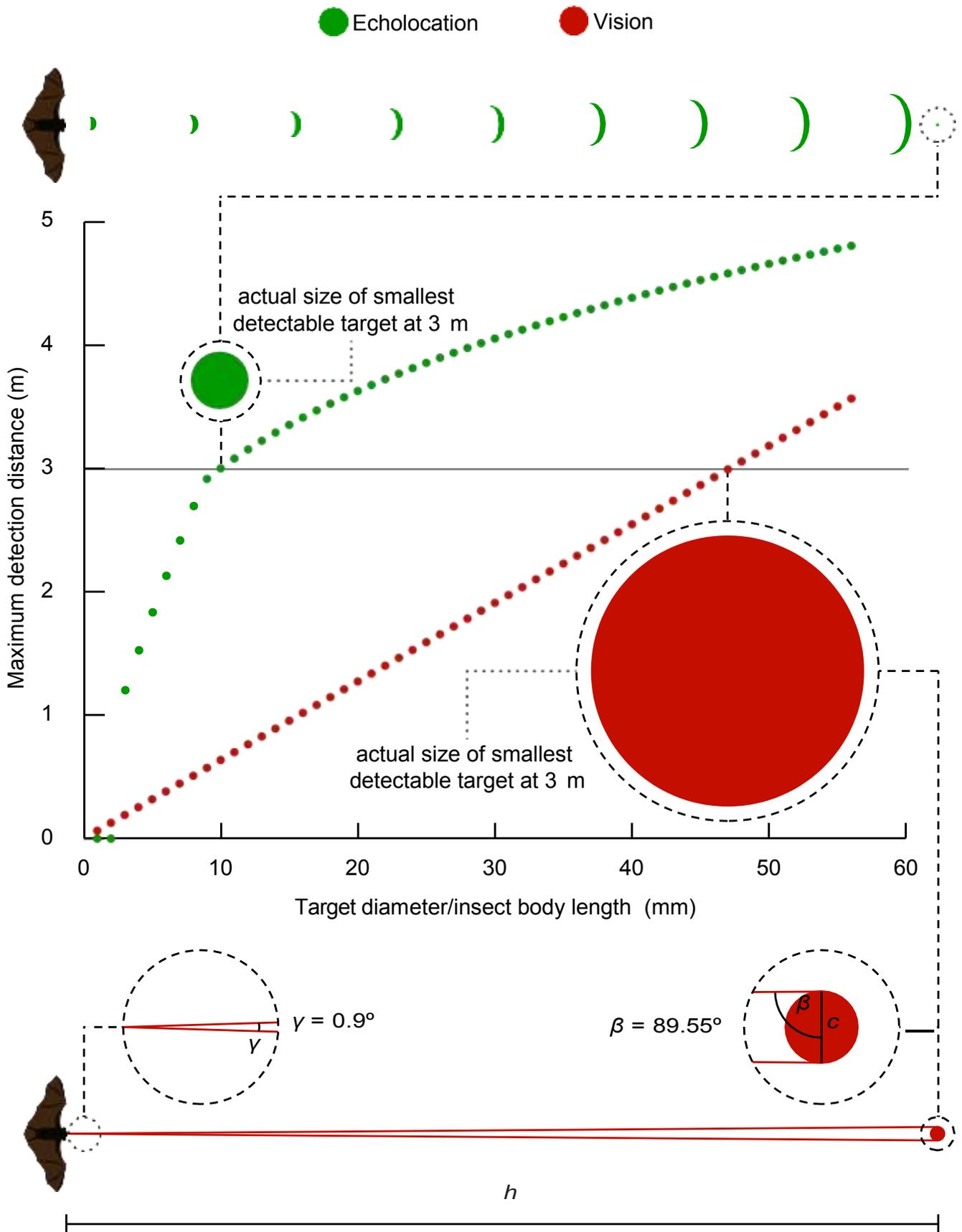


Figure S2. Comparison of model-estimated target detection capabilities of *N. capensis* using vision or echolocation (Appendix S1. b. ii), showing actual sizes (when printed on an A4 size paper) of smallest targets detectable at a 3 m distance away from a bat. Detectability using echolocation is shown for typical atmospheric conditions during our field experiment (20°C; 102,300 Pa; relative humidity 60%). Visual detectability is assumed under ideal lighting conditions and strong visual contrast of target against background.

APPENDIX S1. SUPPLEMENTARY METHODS

a. Echolocation recording and analysis

We used an Anabat™ SD2 (Titley Electronics, Ballina, Australia) to record echolocation activity and AnaLookW™ software for all echolocation data processing. We identified echolocation calls as being produced by *Neoromicia capensis* A. Smith 1829 (Cape serotine bat) through comparisons to echolocation call reference data collected from bats caught during sampling and from Monadjem *et al.* (2010). Only two other species were identified via echolocation recordings: *Tadarida aegyptiaca* E. Geoffroy 1818 (peak echolocation frequency: 22.7 kHz) and *Scotophilus dinganii* A. Smith 1833 (peak echolocation frequency: 33.6 kHz). These three species are easily distinguishable by peak echolocation frequency. It is possible other species with echolocation characteristics similar to *N. capensis* may have been missed when identifying calls. However, we did not catch individuals of any other species with similar calls.

To assess bat foraging activity, we applied an activity index wherein continuous echolocation recordings were subdivided into one-minute intervals (Miller 2001) and the number of one-minute intervals containing *N. capensis* echolocation calls were summed for the entire recording period. The activity index value was standardised for different nights by dividing it by the total time (min) of echolocation recording and multiplying it by 100.

b. Calculation of Selection Probabilities for Prey-Selection Factors

i. Probability of Prey Encounter (R)

If a representative sample of prey is taken from a predator's foraging range, relative proportions of prey should theoretically equal encounter probabilities of different prey. We sampled prey abundance using relatively unbiased methods within bat-foraging range (confirmed by echolocation data) and assumed prey relative abundance approximated prey encounter probability, and calculated the probability of prey encounter as follows:

$$R_{ia} = \frac{N_{ia}}{(N_{ia} + N_{ja} + \dots + N_e)} \quad (\text{eqn S1})$$

where subscript ia , here and hereafter, indicates the prey-selection factor probability and associated variables, calculated for insect order i on the night bat a 's diet was sampled; encounter probability (R_{ia}) equals the number of individuals (N_{ia}) of a prey order divided by the total number of individual prey sampled on the same night. The calculation of R contains no parameters.

ii. Probability of Prey Detection (D)

Prey body lengths were measured for all prey sampled on a night and categorised into body-length classes to the nearest millimetre (sampled prey size ranged from 1–56mm). We then used a modified version of the echolocation model from Safi & Siemers (2010) to estimate detectability of insect orders (all variables are in dB SPL):

$$E_{no\ attenuation} = SL + TS + RAY - DT \quad (\text{eqn S2})$$

where $E_{no\ attenuation}$ is the energy of the returning echo without accounting for atmospheric or geometric attenuation; SL is the source level of the echolocation call which was assumed to be 100 dB; TS is strength of the returned echo calculated from mean body length of a prey order

(equation 4: Safi & Siemers 2010); *RAY* is the sound-energy lost (negative) through Rayleigh scattering when the prey target is smaller than the wavelength of the echolocation call (equation 5 and 6: Safi & Siemers 2010); *DT* is the detection threshold of the bat which was assumed to be 20 dB SPL (Stilz & Schnitzler 2012). Unlike the model from Safi & Siemers (2010), we excluded the effect of the angle of the insect relative to the echolocation beam. We assumed echolocation calls were angled towards the insect to produce maximum sound reflection to allow us to compare different orders of insects to one another.

Our goal was to determine maximum detection distance via echolocation for an insect order on the specific night on which a bat's diet was sampled. We therefore had to determine the distance at which atmospheric and geometric attenuation was equal to $E_{no\ attenuation}$ (i.e., the distance at which the echo is attenuated to the point where it cannot be heard by the bat). We calculated atmospheric attenuation (*TLA* in dB/m) for given atmospheric conditions on the night a particular bat's diet was sampled using a free online calculator (Stilz 2012). Atmospheric conditions were estimated from historical weather data collected from a weather station, 2.59 km from our study site (www.wunderground.com). We calculated geometric attenuation (*TLS*) using equation (2) from Safi & Siemers (2010). We added *TLA* and *TLS* together to calculate the overall attenuation (*TLO*) for 0.1 m increments between 1–6 m from the echo target. We performed a natural log regression of echo target distance and *TLO*. We then combined $E_{no\ attenuation}$ and *TLO* to calculate maximum detection distance (*MDD*). Maximum detection distances for each prey size-class for each sampling night were then standardised (range 0–1) and a regression of size-class and standardised detection distances was used to calculate detectability via echolocation ($D_{(e)}$). The regression took the following form:

$$D_{(e)ia} = c \ln(\overline{bl}_i) - d \quad (\text{eqn S3})$$

where c and d were parameters that varied depending on the atmospheric conditions on a given night. The calculation of $D_{(e)}$ included two parameters.

To estimate the probability of detection by vision (lit conditions), we used the estimated visual acuity of *N. capensis*, 54' (0.9°) of arc (Rydell & Eklöf 2003), to calculate the maximum detection distance of different prey orders. We calculated maximum visual-detection distance of prey using a combination of the sine rule, and Pythagorean theorem on right-angled triangles:

$$h = \sqrt{\left(c \times \frac{\sin \beta}{\sin \gamma}\right)^2 - \frac{1}{4} \times (c)^2} \quad (\text{eqn S4})$$

where h is the height of an isosceles triangle; c is the base, which is the insect's body length; β is the base angle; and γ the vertex angle, which is equal to the visual arc of *N. capensis* (Fig. S2).

Therefore, visual maximum detection distance for prey order i on the night bat a 's diet was sampled ($MDD_{(v)ia}$) is calculated as follows:

$$MDD_{(v)ia} = \sqrt{\left(\bar{bl}_{ia} \times \frac{\sin 89.55}{\sin 0.9}\right)^2 - \frac{1}{4} \times (\bar{bl}_{ia})^2} \times 0.0001 \quad (\text{eqn S5})$$

The result was multiplied by 0.0001 to convert to millimetres to metres.

The combination of echolocation and vision cannot increase the maximum detection distance of prey. The combined maximum detection distance of prey by bats using echolocation and vision, would simply be the higher of two maximum detection distances for vision and echolocation, respectively. It is therefore not logical to add maximum detection distances for vision and echolocation to get a maximum detection distance of prey for vision and echolocation combined. However, the amount of time a bat has to track and capture its prey is a function of maximum detection distance; longer detection distances would allow the bat more time to track and capture its prey. To be conceptually correct, we could convert maximum detection distances

for vision and echolocation to detection/tracking time by assuming bats fly at a constant speed and continuously track their target, and add visual and echolocation tracking time together, to represent the sum of time bats are able to detect prey using vision and echolocation. However, mathematically, this conversion is unnecessary: we can simply add maximum detection distances for vision (v) and echolocation (e) together and standardise the result by taking it as a proportion of the maximum combined detection distances for any prey available to bats during experiments:

$$D_{(ev)ia} = \frac{MDD_{ia(v)} + MDD_{ia(e)}}{\max(MDD_{a(v)} + MDD_{a(e)})} \quad (\text{eqn S6})$$

The probability of detection above assumes all prey targets have similar visual conspicuousness. If light from lamps serves as a visual background, this assumption may be valid, as insects would presumably appear as dark silhouettes against a light background. However, when a bat feeds around lights but is not looking in the direction of lights, darker insects may have lower visual contrast against visual backgrounds. Moths in our study were mostly medium to dark brown, while beetles were mostly dark brown. Moths may therefore be more visually conspicuous than beetles against dark backgrounds. However, beetles may reflect more light than moths as their elytra are shiny. Nevertheless, we included a probability of detection using vision and echolocation where moths were assumed to be three times as conspicuous, visually, as other prey orders ($D_{(ve-lep3)}$). This assumption is likely unrealistic, but provides a robust means of testing whether increased visual information caused moths to be more vulnerable to predation, by testing the visual detection hypothesis in an exaggerated form. The calculation of $D_{(ev)}$ and $D_{(ev-lep3)}$ contained one and two parameters, respectively.

iii. Probability of Capture Given Prey Evasive-Behaviours (E)

The probability of capture given prey escape behaviours was calculated as follows:

$$E_{(ee)ia} = \frac{N_{ia} - \left(Ne_{ia} \times \frac{ee}{100} \right)}{N_{ia}} \quad (\text{eqn S7})$$

where N_{ia} is the number of all individuals from an insect order; Ne_{ia} is the number of eared individuals from that order; ee is the percentage efficacy-estimate of defensive behaviours (20, 40, 60, 80). $E_{(ee)ia}$ is therefore the proportion of individuals in a prey order which are un-eared as well as eared-individuals for which defensive behaviours are expected not to be effective against predation.

Some insects from orders other than Lepidoptera (e.g., Coleoptera, Mantodea, Neuroptera, Orthoptera) have also evolved ears and some are known to exhibit anti-bat defensive behaviours in response to ultrasound (Conner & Corcoran 2012). We used the same percentage efficacy values for all eared insects known to exhibit anti-bat defensive behaviours, but this assumption had very little impact on model outcome. The calculation of E contains one parameter.

iv. Probability of Prey Being Actively Selected by the Predator (A)

We assumed that preference for prey based on size would scale linearly with prey size (Cunningham, Ruggerone & Quinn 2013). We standardised this relationship by assuming the largest insect captured during prey availability assessment on all nights (body length of 56 mm), was the prey item most likely to be captured by bats. Size-based preference based on size was calculated as follows:

$$PP_{(s)ia} = \left(\overline{bl}_i \times \frac{1}{56} \right) \quad (\text{eqn S8})$$

where mean size (body length (mm)) of an insect order was multiplied by 1/56.

To estimate energy content for different prey orders, we combined body-length measurements of prey sampled during experiments and body-length-to-mass regression models with mass-specific, energy-content data (Sabo, Bastow & Power 2002; Rumpold & Schlüter 2013) to estimate mean energy content per capture for a specific insect order on a given night (see Table S1 for a summary of energy content for different insect orders). We then calculated prey preference based on prey energy content $PP_{(e)ia}$ as follows:

$$PP_{(e)ia} = \left(\frac{\text{mean energy content per capture}_{ia}}{\text{maximum energy content per capture measured}} \right) \quad (\text{eqn S9})$$

A predator should become more selective for prey when foraging in a patch of high quality (MacArthur & Pianka 1966). It is therefore not sufficient to simply calculate probabilities of active selection based on preferences for prey size or energy content in isolation. The perceived quality of the patch within which the predator forages must be taken into account. When a predator perceives a patch as high quality, it should become more selective for high-quality prey, thereby altering its prey-preference. We theorised that bats in our study would perceive patch quality as a product of prey density and prey size/energy-content. In the context of our experiment, patch quality refers to the density and quality of prey available to a bat as sampled at our experimental site, on the night a particular bat's diet was sampled. We did not measure prey density directly. Instead, we used time-standardised sampling rate (sr_{ia} : number of insects from order i sampled per hour on the night bat a 's diet was sampled) as a proxy for prey density on a given night. A simple metric for patch quality, in this case for size-based selection, could then be calculated as follows:

$$PQ_{(s)a} = \sum_{i=\text{insect order } 1}^{\text{insect order } 9} \overline{bl}_{ia} \times sr_{ia} \quad (\text{eqn S10})$$

where patch quality ($PQ_{(s)a}$) equals the sum of mean body-length (in the case of energy-based selection, mean energy content would be used instead) measured for prey order i on the night bat a 's diet was sampled, multiplied by the sampling rate (sr_{ia}) for the same prey order on the same night. Patch quality is therefore a measure of the density and quality of all prey available to a bat on a particular night. To adjust bat preferences for prey given patch quality, we had to scale patch quality on a given night relative to the highest patch quality recorded for a night during experiments, for which we assumed selective preferences would be strongest. Relative patch quality, in this case based on size-based selection, was then calculated as follows:

$$RPQ_{(s)a} = \frac{\ln(PQ_{(s)a})}{\ln(\max PQ_{(s)a})} \quad (\text{eqn S11})$$

We take the natural log of patch quality as we expect selectivity to show a natural log relationship with density (Cunningham, Ruggerone & Quinn 2013). Relative patch quality for energy-based selection would be calculated as above but with energy-based patch quality metrics. Finally, the probability of active selection, in this case based on size, was calculated as follows:

$$A_{(s)ia} = PP_{(s)ia}^{RPQ_{(s)a}} \quad (\text{eqn S12})$$

where the probability of active selection of prey order i based on prey size ($A_{(s)ia}$), is the preference for prey order i , based on its size, to the power of the relative patch quality ($RPQ_{(s)a}$) on the night that bat a was foraging. In this way, the higher relative patch quality becomes, the more linear the relationship between preference for prey and prey size/energy-content becomes. Therefore, when patch quality is low, predators prefer medium- and high-quality prey relatively equally. When patch quality is high, the difference in preference between medium and high quality prey becomes more pronounced, and bats would be more likely to select only high quality prey.

v. Probability of Prey Being Selected by the Predator Based on Handling Constraints (H)

The primary physical constraint to consumption is the ability of bats to chew and swallow prey. We therefore estimated gape-size for each bat and excluded all individual prey that were larger than a bat's gape from further calculations of H for an insect order. We also adjusted for the reduced availability of prey which were too large for a bat's gape within an order by creating a simple gape limitation index ($h_{(g)}$) by which to adjust H . To estimate gape-size for bats, we used data from Monadjem *et al.* (2010) to calculate a relationship between cranial length and forearm length for male and female *N. capensis*, respectively. We then estimated cranial length for each bat using the following equations:

$$CL_a = CL_l \times \left(\frac{FA_a}{FA_l} \right) \quad (\text{eqn S13})$$

where estimated cranial length for bat a (CL_a) is equal to mean cranial length for bat a 's sex (CL_l), multiplied by the ratio between bat a 's forearm length (FA_a) and mean forearm length for bat a 's sex (FA_l). Therefore, estimated cranial length for bat a is an individual size-adjustment of mean cranial length taken from Monadjem *et al.* (2010). We further estimated the distance between the temporomandibular joint and apexes of the upper and lower canines, respectively by calculating the ratio between cranial length and both of the aforementioned distances from museum specimen photographs from Monadjem *et al.* (2010). We subsequently calculated the distance between upper and lower canines using standard trigonometric calculations for each individual bat. We assumed the maximum gape angle was 45° for all bats (Dumont 2003). All insects estimated to be larger than an individual bat's gape size were excluded from further calculations of H for that bat. Apart from excluding them from further H calculations, the reduced availability based on gape constraints must be reflected in H . To do this, we created a simple gape limitation index ($h_{(g)}$) by which to adjust H . The index was calculated as the number

of individuals in an order that fit inside the gape of a particular bat over the total number of individuals in that order caught on the night in question. Therefore, the fewer individuals that a bat was able to consume, the lower $h_{(g)ia}$, and the lower the probability of H becomes.

Insect hardness may also affect the ability of bats to consume prey, however, bite forces estimated for bats (Aguirre *et al.* 2002; Freeman & Lemen 2007) greatly exceeded forces required to chew insects in our study.

The ability of bats to physically handle and manoeuvre prey in flight also needs to be considered. There are no reliable data on the maximum size of prey aerial-hawking bats are able to handle in flight. We therefore scaled handling difficulty of prey as the largest body dimension (length, height, or width) of the insect relative to a bat's forearm length, resulting in the ease of handling index ($h_{(h)}$) which was calculated as follows:

$$h_{(h)ia} = 1 - \left(\frac{\max dim.i}{fa_a \times 2} \right) \quad (\text{eqn S14})$$

where the mean maximum dimension of an insect order (mm) was divided by twice the forearm length (mm) of the bat and then subtracted from 1. If the maximum dimension of an insect exceeded twice the forearm length, $h_{(h)}$ was zero. Finally, H was calculated as follows:

$$H_{ia} = h_{(g)ia} \times h_{(h)ia} \quad (\text{eqn S15})$$

The calculation of H contained four parameters.

References

- Aguirre, L.F., Herrel, A., van Damme, R. & Matthysen, E. (2002) Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1271–1278.
- Conner, W.E. & Corcoran, A.J. (2012) Sound strategies: the 65 million-year-old battle between bats and insects. *Annual Review of Entomology*, **57**, 21–39.

- Cunningham, C.J., Ruggerone, G.T. & Quinn, T.P. (2013) Size selectivity of predation by brown bears depends on the density of their sockeye salmon prey. *The American Naturalist*, **181**, 663–673.
- Dumont, E.R. (2003) The effects of gape angle and bite point on bite force in bats. *Journal of Experimental Biology*, **206**, 2117–2123.
- Freeman, P.W. & Lemen, C.A. (2007) Using scissors to quantify hardness of insects: do bats select for size or hardness? *Journal of Zoology*, **271**, 469–476.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist*, **100**, 603–609.
- Miller, B.W. (2001) A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, **3**, 93–105.
- Monadjem, A., Taylor, P.J., Cotterill, F.P.D. & Schoeman, M.C. (2010) *Bats of Southern and Central Africa: A Biogeographic and Taxonomic Synthesis* (eds A Monadjem, PJ Taylor, FPD Cotterill, and MC Schoeman). Wits University Press, Johannesburg.
- Rumpold, B.A. & Schlüter, O.K. (2013) Nutritional composition and safety aspects of edible insects. *Molecular Nutrition & Food Research*, **57**, 802–823.
- Rydell, J. & Eklöf, J. (2003) Vision complements echolocation in an aerial-hawking bat. *Naturwissenschaften*, **90**, 481–4833.
- Sabo, J.L., Bastow, J.L. & Power, M.E. (2002) Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, **21**, 336–343.
- Safi, K. & Siemers, B. (2010) Implications of sensory ecology for species coexistence: biased perception links predator diversity to prey size distribution. *Evolutionary Ecology*, **24**, 703–713.
- Stilz, W.-P. (2012) Echolocation range calculator, <http://134.2.91.93/~peter/calculator/range.php>
- Stilz, W.-P. & Schnitzler, H.-U. (2012) Estimation of the acoustic range of bat echolocation for extended targets. *The Journal of the Acoustical Society of America*, **132**, 1765–75.

Table S1. Body length, estimated energy content, estimated maximum detection distance, and sampling rate shown for all insects captured during unlit and lit conditions, respectively. Values are mean \pm standard deviation.

	Body Length (mm)		Estimated Energy Content per Individual (J)		Estimated Maximum Detection Distance (m)		Sampling Rate (individuals/hour)	
	Unlit	Lit	Unlit	Lit	Unlit	Lit	Unlit	Lit
Lepidoptera	17.4 \pm 6.6	17.2 \pm 4.6	565 \pm 42	554.1 \pm 16.0	3.46 \pm 0.03	3.48 \pm 0.04	6.2 \pm 1.9	29.0 \pm 8.7
Coleoptera	15.6 \pm 8.2	14.2 \pm 3.7	1150 \pm 212	893.6 \pm 25.6	3.13 \pm 0.08	3.21 \pm 0.06	7.1 \pm 2.5	25.7 \pm 18.4
Diptera	3.5 \pm 1.9	3.45 \pm 1.6	9 \pm 2	9.4 \pm 1.7	1.45 \pm 0.13	1.52 \pm 0.09	24.3 \pm 4.1	207.2 \pm 94.7
Trichoptera	3.2 \pm 0.4	3.5 \pm 0.9	5 \pm 0	6.5 \pm 0.1	1.37 \pm 0.00	1.42 \pm 0.46	0.6 \pm 0.5	16.6 \pm 9.7
Orthoptera	32.3 \pm 2.3	32.0 \pm 2.0	3861 \pm 4	3769.7 \pm 3.2	4.25 \pm 0.00	4.27 \pm 0.00	0.4 \pm 0.7	0.1 \pm 0.3
Hemiptera	6.1 \pm 3.5	5.8 \pm 3.1	41 \pm 7	34.5 \pm 4.3	2.16 \pm 0.24	2.09 \pm 0.14	1.6 \pm 1.8	3.5 \pm 1.2
Neuroptera	9.5 \pm 2.2	10.8 \pm 1.0	228 \pm 5	317.3 \pm 2.5	2.73 \pm 0.00	2.98 \pm 0.13	0.7 \pm 1.2	0.3 \pm 0.16
Hymenoptera	5.9 \pm 2.1	7.5 \pm 2.2	184 \pm 38	265.7 \pm 38.3	2.19 \pm 0.13	2.47 \pm 0.06	1.3 \pm 1.7	0.5 \pm 0.3
Mantodea	40.3 \pm 4.5	42.5 \pm 1.67	10276 \pm 32	11791.6 \pm 2.5	4.5 \pm 0.00	4.23 \pm 1.33	0.1 \pm 0.2	0.5 \pm 0.2

Table S2. Selection probability factors* included in all models tested shown with number of parameters for each

Model Number	Number of Parameters	Selection Probability Factors				
		<i>R</i>	<i>D</i>	<i>E</i>	<i>A</i>	<i>H</i>
1	6	x	<i>e</i>	<i>abs.</i>	-	x
2	7	x	<i>e</i>	20	-	x
3	7	x	<i>e</i>	40	-	x
4	7	x	<i>e</i>	60	-	x
5	7	x	<i>e</i>	80	-	x
6	8	x	<i>e</i>	<i>abs.</i>	<i>s</i>	x
7	8	x	<i>e</i>	<i>abs.</i>	<i>e</i>	x
8	9	x	<i>e</i>	20	<i>s</i>	x
9	9	x	<i>e</i>	40	<i>s</i>	x
10	9	x	<i>e</i>	60	<i>s</i>	x
11	9	x	<i>e</i>	80	<i>s</i>	x
12	9	x	<i>e</i>	20	<i>e</i>	x
13	9	x	<i>e</i>	40	<i>e</i>	x
14	9	x	<i>e</i>	60	<i>e</i>	x
15	9	x	<i>e</i>	80	<i>e</i>	x
1 _(ev)	7	x	<i>ev</i>	<i>abs.</i>	-	x
2 _(ev)	8	x	<i>ev</i>	20	-	x
3 _(ev)	8	x	<i>ev</i>	40	-	x
4 _(ev)	8	x	<i>ev</i>	60	-	x
5 _(ev)	8	x	<i>ev</i>	80	-	x
6 _(ev)	9	x	<i>ev</i>	<i>abs.</i>	<i>s</i>	x
7 _(ev)	9	x	<i>ev</i>	<i>abs.</i>	<i>e</i>	x
8 _(ev)	10	x	<i>ev</i>	<i>abs.</i>	-	x
9 _(ev)	10	x	<i>ev</i>	20	-	x
10 _(ev)	10	x	<i>ev</i>	40	-	x
11 _(ev)	10	x	<i>ev</i>	60	-	x
12 _(ev)	10	x	<i>ev</i>	80	-	x
13 _(ev)	10	x	<i>ev</i>	<i>abs.</i>	<i>s</i>	x
14 _(ev)	10	x	<i>ev</i>	<i>abs.</i>	<i>e</i>	x
15 _(ev)	10	x	<i>ev</i>	20	<i>s</i>	x

Table S2. Continued

Model Number	Number of Parameters	Selection Probability Factors				
		<i>R</i>	<i>D</i>	<i>E</i>	<i>A</i>	<i>H</i>
1 _(ev-lep3)	8	x	<i>ev-lep3</i>	<i>abs.</i>	-	x
2 _(ev-lep3)	9	x	<i>ev-lep3</i>	20	-	x
3 _(ev-lep3)	9	x	<i>ev-lep3</i>	40	-	x
4 _(ev-lep3)	9	x	<i>ev-lep3</i>	60	-	x
5 _(ev-lep3)	9	x	<i>ev-lep3</i>	80	-	x
6 _(ev-lep3)	10	x	<i>ev-lep3</i>	<i>abs.</i>	<i>s</i>	x
7 _(ev-lep3)	10	x	<i>ev-lep3</i>	<i>abs.</i>	<i>e</i>	x
8 _(ev-lep3)	11	x	<i>ev-lep3</i>	20	<i>s</i>	x
9 _(ev-lep3)	11	x	<i>ev-lep3</i>	40	<i>s</i>	x
10 _(ev-lep3)	11	x	<i>ev-lep3</i>	60	<i>s</i>	x
11 _(ev-lep3)	11	x	<i>ev-lep3</i>	80	<i>s</i>	x
12 _(ev-lep3)	11	x	<i>ev-lep3</i>	20	<i>e</i>	x
13 _(ev-lep3)	11	x	<i>ev-lep3</i>	40	<i>e</i>	x
14 _(ev-lep3)	11	x	<i>ev-lep3</i>	60	<i>e</i>	x
15 _(ev-lep3)	11	x	<i>ev-lep3</i>	80	<i>e</i>	x

**R* = probability of prey encounter; *D* = probability of detection (*e* indicates detectability of prey using echolocation; *ev* indicates detectability using a combination of echolocation and vision; *ev-lep3* indicates detectability of prey using a combination of echolocation and vision with the assumption that Lepidoptera are three times more visually conspicuous than other prey orders); *E* = probability of capture given prey evasive-behaviour with percentage efficacy (*abs.*, 20, 40, 60, 80) of defensive behaviours indicated in table; *A* = probability of prey being actively selected by the predator based on energy (*e*) and size (*s*); *H* = probability of prey being selected by the predator based on handling constraints